



Effects of altitude, seedfall and control operations on rat abundance in South Island *Nothofagus* forests 1998–2016

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Abstract: In New Zealand, ship rats (*Rattus rattus*) have been implicated in many extinctions, declines, and range contractions of native birds, so ship rats are an important target of predator control. The outcomes of ship rat control operations are difficult to predict due to other factors which affect rat populations including altitude, *Nothofagus* seedfall, and control of other mammalian pests, particularly brushtail possums (*Trichosurus vulpecula*) and stoats (*Mustela erminea*). Here we used long-term rat tracking-tunnel data 1998–2016 from seven *Nothofagus* forest sites in the northern South Island to address three questions: (1) How do rat tracking rates vary with altitude and *Nothofagus* seedfall? (2) Which forms of rat control are more effective at reducing rat tracking rates? (3) Is there evidence for mesopredator release of rats in *Nothofagus* forests when stoats are controlled by trapping? Analysis with binomial GLMMs found that rat tracking rates significantly declined with altitude and increased with *Nothofagus* seedfall, especially during high-seed years in 2000, 2006, and 2014. Diphacinone, and especially brodifacoum and aerially applied 1080, significantly reduced rat tracking rates, whereas intensive snap-trapping did not. Contrary to earlier studies from North Island forests, we found that rat tracking rates increased significantly with mustelid trapping, suggesting mesopredator release of rats following stoat control. Therefore, in *Nothofagus* forests where rats are present, land managers should consider the relative threats to native wildlife from stoats and ship rats when deciding whether to trap stoats in an area without effectively controlling ship rats. This study highlights the value of long-term data sets for identifying relationships that may otherwise go undetected.

Keywords: Aerial 1080, altitude, beech forest, competitive release, mast seeding, mesopredator release, *Mustela erminea*, pest control, *Rattus rattus*, *Trichosurus vulpecula*

Introduction

Predation by introduced mammals is considered the leading cause of decline for native birds in New Zealand forests (Clout 2001; Innes et al. 2010). Within the suite of introduced predators, ship rats (*Rattus rattus*) are one of the more ubiquitous species and have been implicated in many of the extinctions, declines, and range contractions of native birds (Tennyson & Martinson 2006; Innes et al. 2010; Brown et al. 2015), and therefore ship rats are one of the main targets of predator control in New Zealand. A variety of pest management methods have been used to control ship rat populations in New Zealand southern beech (*Nothofagus* spp) forests with varying degrees of success. The outcomes of ship rat control operations are difficult to predict due to additional factors that may contribute to changes in rat populations, including altitude, temperature, beech seedfall, and control of other mammalian pests, particularly brushtail possums (*Trichosurus vulpecula*) and stoats (*Mustela erminea*).

Toxic baits including sodium fluoroacetate (1080),

brodifacoum, diphacinone, and pindone have been used to control invasive rodent populations in New Zealand for many years (Eason et al. 2011), either by aerial or ground-based application. Snap traps were also commonly used to control rats in the past, but it has generally been concluded that trapping alone is unable to control ship rats to low enough levels for effective native bird conservation (Ogden & Gilbert 2009; Brown et al. 2015). Control operations using brodifacoum, whether in bait stations or aerially sown, have been highly successful. Aerially applied brodifacoum is used to eradicate rats from islands (Russell & Broome 2016) and mainland predator proof fenced sanctuaries (Innes et al. 2012). Brodifacoum has been more successful than other toxins i.e. diphacinone and pindone, at reducing rat populations on the mainland (North and South Islands) (Gillies et al. 2003; Parkes et al. 2011). However, as brodifacoum is persistent, its use for conservation is now restricted on the mainland due to build-up in the food chain with consequent risks of non-target mortality (Eason & Spurr 1995; Eason et al. 1999; Innes & Barker 1999). Aerially applied 1080 has been effective at

rat control on mainland New Zealand with lower non-target effects (Elliott & Kemp 2016). Pest control with 1080 is advantageous because it has a much higher LD₅₀ (lethal dose) for native birds than introduced mammals (e.g. 1.2 mg kg⁻¹ for ship rats compared to 6.0 mg kg⁻¹ for weka *Gallirallus australis*), is biodegradable, and can be applied aerially over extensive geographic areas (Eason et al. 2011; Elliott & Kemp 2016; Parkes et al. 2017). For these reasons the New Zealand Department of Conservation (DOC) used large-scale aerial 1080 for pest control (called Tiakina Ngā Manu/ Battle for our Birds) during the geographically extensive beech mast seeding events that took place in 2014 (Elliott & Kemp 2016), 2016, and 2019.

Mast seeding (synchronous highly variable seed production among years by a population of perennial plants) is common in New Zealand and occurs over large geographic areas (Kelly 1994; Schaubert et al. 2002; Kelly et al. 2008; Kelly et al. 2013; Pearse et al. 2016). The four dominant *Nothofagus* taxa – red beech (*Nothofagus fusca*, syn *Fuscospora fusca*, Heenan & Smissen 2013), silver beech (*N. menziesii*), mountain beech (*N. solandri* var. *cliffortioides*) and black beech (*N. solandri* var. *solandri*), exhibit strong mast seeding in broad synchrony across hundreds of kilometres (Schauber et al. 2002). Heavy beech seed production during mast years is associated with irruptions of rodents (house mouse *Mus musculus* and rat *Rattus* spp. especially ship rats) and stoats (King 1983; King & Moller 1997; Dilks et al. 2003), with consequent increased predation on native birds (Elliott 1996; O'Donnell 1996; Elliott & Kemp 2016). The increase in ship rat abundance in high-seed years is well known, but less is known about how this varies across altitudinal gradients or with pest control methods.

The elevational distribution of ship rat populations within New Zealand *Nothofagus* forests has been recently documented, but how this interacts with seedfall and management is not well known. Griffiths & Barron (2016) found that rat tracking rates (% of tracking tunnels with rat sign) in New Zealand forest were lower in higher-altitude beech forests than lower-altitude podocarp forests. Walker et al. (2019) showed that across all of New Zealand, rats were more common at lower-altitude and warmer sites, and were more irruptive in cool-climate *Nothofagus* forest types, but they said more information was needed to understand how management interacts with these drivers. Ship rat trap-capture rates increased with beech seedfall and declined with altitude in beech forest at Mt Misery, Nelson Lakes National Park (Christie et al. 2017) and in Craigieburn Forest Park, Canterbury (Harris et al. 2022). *Nothofagus* seedfall shows a continuous distribution of crop sizes from very low to very high, so any division into categories is arbitrary (Wardle 1984 p 257; Kelly 1994) but seed crops over 2000 seeds m⁻² are almost certain to trigger rodent outbreaks (Elliott & Kemp 2016). Interestingly, at Craigieburn ship rats had been almost completely absent 1973–2003, but invaded after 2009 associated with increasing winter temperatures (Harris et al. 2022). In the Hollyford Valley, Carpenter et al. (2022) tested whether low temperatures or lack of food limited rat abundance at high altitudes; supplementary feeding slowed, but did not prevent, the decline in rats near the treeline after a mast year. However, it is not known how pest control operations interact with beech masting and altitude, because Christie et al. (2017) and Carpenter et al. (2022) had no pest-control sites, while Harris et al. (2022) had no non-treatment sites. It is important to determine how seedfall and altitude may contribute to changes in the outcomes of predator control operations, in order to maximise the benefits for native bird conservation.

Mesopredator release occurs when an apex predator is controlled and this causes populations of its prey (a mesopredator) to increase because of reduced predation (Soule 1988). Similarly, competitive release may occur when one pest species is controlled, allowing populations of another pest species from the same trophic level to increase due to reduced competition (Caut et al. 2007). In mixed forests in the North Island of New Zealand, several studies have found evidence for competitive release of ship rats following brushtail possum control (Sweetapple & Nugent 2007; Ruscoe et al. 2011; Griffiths & Barron 2016), which is likely a consequence of reduced competition for seeds and fruit (Sweetapple & Nugent 2007). Ruscoe et al. (2011) also tested for mesopredator release but found that rat abundance did not significantly increase with stoat removal. In contrast, modelling studies have predicted ship rat increases in mixed *Nothofagus* forests through mesopredator release when stoats were controlled (Blackwell et al. 2001; Tompkins & Veltman 2006). The latter is consistent with anecdotal reports from North and South Island kiwi management sites that ship rats may increase when stoats are controlled (Robertson et al. 2011; Robertson & De Monchy 2012).

Our aim in this paper is to use long-term data from seven different sites in the northern South Island to investigate factors affecting rat tracking-tunnel rates. Specifically, we address three questions. (1) How do rat tracking rates vary with altitude and *Nothofagus* seedfall? (2) Which forms of rat control are the most effective at reducing rat tracking rates? (3) Is there evidence for mesopredator release of rats in *Nothofagus* forests when stoats are controlled by trapping?

Methods

Study sites

Six treatment sites and one non-treatment site were used in this study (see Table 1 for co-ordinates). Nelson Lakes National Park contains four treatment sites (Rotoiti in the core treatment area near St Arnaud, Lakehead, Big Bush, and Black Valley), and the adjacent non-treatment site (Rotoroa), which have been managed by DOC since 1997 under the Rotoiti Nature Recovery Project (RNRP). The sites carry old-growth cool-temperate southern beech forest, and average annual rainfall varies between 1100 and 3000 mm depending on altitude (Elliott et al. 2010; Christie et al. 2017). The canopy here is dominated by red and silver beech with matai (*Prumnopitys taxifolia*), kahikatea (*Dacrycarpus dacrydioides*) and kāmahi (*Pterophylla racemosa*), with increasing abundance of mountain beech nearer to the treeline (c. 1425 m a.s.l.) (Beggs & Wilson 1991).

The remaining two treatment sites (Cobb and Flora) are located in Kahurangi National Park, near the Arthur/Wharepapa Range and Tablelands. The canopy in the low- and mid-slopes is dominated by silver beech with scattered areas of red beech and small patches of southern rātā (*Metrosideros umbellata*) with a typical understory of *Griselinia littoralis*, *Pseudopanax* spp., and *Coprosma* spp. (Wardle 1984; Masuda et al. 2014). Nearer the treeline (1300–1400 m a.s.l.) the canopy is dominated by silver and mountain beech.

Predator control

Predator control within the study areas has varied across sites and years, as detailed below and summarised in Table 1. Control

Table 1. Site locations and pest control methods used each year to control brushtail possums, stoats and ship rats (in order, separated by commas) during the study period. A = aerial 1080 treatment, B = brodifacoum, C = cyanide, D = diphacinone, H = hand-laid 1080, T = targeted trapping, and 0 = no targeted treatment. Blank cells are site/years not used in this study, and there were no tracking tunnel data for 2001 and for Black Valley in 2005, 2007/11. 0*, aerial 1080 applied after monitoring. (0), a minority of area treated with aerial 1080 but analysed as untreated, see text.

Site	Rotoroa	Rotoiti	Lakehead	Big Bush	Black Valley	Cobb	Flora
Latitude S	41.92°	41.82°	41.83°	41.79°	41.80°	41.13°	41.18°
Longitude E	172.67°	172.86°	172.83°	172.84°	172.88°	172.61°	172.73°
1998	0, 0, 0	B, T, B	0, 0, 0				
1999	0, 0, 0	B, T, B	0, 0, 0				
2000	0, 0, 0	T+C, T, T	0, 0, 0				
2001	0, 0, 0	T+C, T, T	0, T, 0				
2002	0, 0, 0	T+C, T, T	0, T, 0	0, T, T	0, T, 0		
2003	0, 0, 0	T, T, T	0, T, 0	0, T, T	0, T, 0		
2004	0, 0, 0	T, T, T	0, T, 0	0, T, T	0, T, 0		
2005	0, 0, 0	T, T, T	0, T, 0	0, T, T	0, T, 0		
2006	0, 0, 0	T+H, T, H	0, T, 0	0, T, 0	0, T, 0		
2007	0, 0, 0	T, T, 0	0, T, 0	0, T, 0	0, T, 0		
2008	0, 0, 0	T, T, 0	0, T, 0	0, T, 0	0, T, 0		
2009	0, 0, 0	T, T, 0	T, T, 0	0, T, 0	0, T, 0		
2010	0, 0, 0	T, T, D	T, T, 0	0, T, 0	0, T, 0		
2011	0, 0, 0	T, T, D	T, T, 0	0, T, 0	0, T, 0		
2012	0, 0, 0	T, T, D	T, T, D	0, T, 0	0, T, 0		
2013	0, 0, 0	T, T, P	T, T, P	T, T, 0	T, T, 0	T, T, 0	T, T, (0)
2014	0, 0, 0	T, T, A	T, T, A	T, T, 0	T, T, 0	T, T, 0*	T, T, A
2015	0, 0, 0	T, T, 0	T, T, 0	T, T, 0	T, T, 0	T, T, 0	T, T, 0
2016	0, 0, 0	T, T, 0	T, T, 0	T, T, 0	T, T, 0	T, T, 0*	T, T, A

has largely been undertaken by DOC and the community groups Friends of Rotoiti (FOR), Friends of Cobb (FOC), and Friends of Flora (FOF).

Brushtail possums have been targeted by these organisations using a range of trapping and toxin applications (brodifacoum, cyanide, and 1080) within the treatment sites (Table 1). At Rotoiti the rat bait station network (described below) was used for targeted poisoning of possums with brodifacoum in 1998 and 1999, followed by poisoning with cyanide and/or trapping with Victor No 1 leg-hold traps and/or kill traps (BMI 160, Warrior and Sentinel) and poisoning with 1080 in 2006, along buffer lines around the Rotoiti site until 2009 when these increased to include lines within the Rotoiti site and extended to include Lakehead (Table 1). Possum trap lines in the RNRP were extended again in 2013 to include buffer lines around Big Bush and Black Valley. Possum densities within the RNRP treatment sites were also likely reduced by nearby Animal Health Board (AHB) control operations in forests to the north of Big Bush between December 2001 and June 2007 using various toxins. In Kahurangi National Park, possum trapping used c. 400 Sentinel kill traps in Flora and c. 40 in Cobb, resulting in possum detection at these sites at or near zero during the course of this study.

Stoat control in the RNRP used Fenn traps set 50–100 m apart, covering 825 ha in Rotoiti from 1998 to 2008 and extended to 5000 ha to include all monitoring lines in Lakehead, Big Bush, and Black Valley in August 2001 (Table 1). In 2008 the Fenn traps were replaced with a mixture of DOC 200 and DOC 250 traps. Stoat traplines in Flora and Cobb also use DOC 200s covering a total area of 8000 ha each, with traps along lines spaced 50 m apart in Flora and 100–200 m in Cobb.

Ship rats have been targeted with a range of trapping and toxin applications (Table 1). Bait stations for rat control in Rotoiti covered 825 ha, set on a 100 m by 100 m grid. These

were used for brodifacoum in 1998 and 1999 and then Victor Professional break-back snap traps set along the existing bait station lines from 2000 to 2005 and extended to include Big Bush monitoring lines from 2001 to 2005, totalling a managed area of c. 1100 ha (Table 1). In 2006, 500 ha of the bait station network was used for poisoning with ground-applied 1080 which included 7 of 10 monitoring lines in Rotoiti. In 2010 and 2011, 867 ha of the bait station network was used for diphacinone treatment in Rotoiti (including all Rotoiti monitoring lines) and repeated in 2012 with diphacinone together with an extension to include the Lakehead site, and then similarly treated with pindone in 2013.

Aerial 1080 operations targeting ship rats took place in Rotoiti and Lakehead on 3 December 2014 (8 days before mammal monitoring), Flora on 14 November 2013 (5 days before monitoring), August 2014, 7–8 November 2014 (5 days before) and 8–24 November 2016 (9 days before), and in Cobb on 7–8 November 2014 (5 days after monitoring) and 8–24 November 2016 (2 days after). The aerial operation in Flora in 2013 only covered a small portion of the study area (4 of the 12 monitoring lines) so we counted this as a non-rat-treatment site in 2013. We analysed Cobb as a non-rat-treatment site in 2014 and 2016 because aerial 1080 application occurred after wildlife monitoring was complete.

Monitoring methods

Permanent tracking lines were installed for long-term monitoring at all sites by DOC, FOF, and FOC. Rodent monitoring was carried out using Black Trakka cards (Gotcha Traps Ltd, Auckland) set in 600 mm long black corflute tunnels, with a peanut butter lure applied to both ends, set for one rainless night. Each tracking tunnel line included 10 individual tracking tunnels spaced 50 m apart, and lines were placed within the stoat-trapping networks at all treatment sites

except for 5 of 10 lines in Cobb that began on the trapline in the valley floor and continued uphill away from the trapline. The number of tunnels monitored at Big Bush (40 tunnels), Lakehead (40), Cobb (100) and Flora (120) was consistent each year whereas the number of tunnels monitored varied over time at Rotoiti (80–100), Black Valley (20–60), and Rotoroa (100–160 tunnels). This study used tracking tunnel data collected in November (or as close to as possible) from 1998 to 2016 in Rotoroa, Rotoiti and Lakehead, 2002 to 2016 in Big Bush and Black Valley and 2013 to 2016 in Cobb and Flora (Table 1). There were some tracking tunnel data gaps, including for Rotoroa, Rotoiti and Lakehead in November 2001, and for Black Valley in 2005 and 2007 to 2011. Monitoring was undertaken by DOC and the University of Canterbury.

Twenty 0.28 m² seed traps were used to measure annual beech seed production every year at Rotoroa and Rotoiti and eight seed traps of the same size at Flora. Monitoring of seed traps was undertaken by DOC. We used total seeds m⁻² for all beech species combined.

Statistical analysis

We used a binomial generalised linear mixed model (GLMM) to model the response of ship rat tracking rates to fixed terms for stoat treatment, possum treatment, rat treatment, altitude, beech seedfall and previous rat tracking rates across all sites, using the *glmmTMB* package (Brooks et al. 2017) in R version 3.5.1. Random terms were fitted for individual tracking tunnels nested within transects within sites.

Altitude (km a.s.l.) and seedfall (mean beech seeds m⁻²) were included in the model as continuous variables. Counts were total seed (not just sound seed) for all three species combined (*N. solandri*, *N. fusca*, and *N. menziesii*) and were log-transformed (log₁₀) to allow for the right-skewed nature of the seed data. Seedfall data were only available from three locations (Rotoiti, Rotoroa, and Flora), so data from Rotoiti were used for the nearby Big Bush, Black Valley, and Lakehead sites, and Flora seedfall data used for the nearby Cobb site.

Both stoat and possum treatment terms included two levels (treatment and non-treatment). We initially ran the model with four levels for possum treatment (brodifacoum, trapping, trapping with toxin application, and non-treatment) but this was reduced to two levels after initial data exploration indicated that the extra treatment levels gave little additional information, perhaps because of few replicates of some of the treatments. Possum treatment with brodifacoum showed a strong negative effect on rat tracking rates, but this was probably because rats were also targeted with brodifacoum in the same years (1999 and 2000), and the remaining possum treatments showed no effect on rat tracking rates.

Rat treatment included six levels: aerial 1080, brodifacoum, diphacinone, other toxins, trapping and non-treatment. The 'other toxins' level combined pindone and hand-laid 1080 because these were each only applied in one year during this study (Table 1) so lacked enough replication for separate analysis.

Previous rat tracking rates were included as a predictor, using the mean tracking rate per site during November in the previous year. Mustelid tracking data (proportion of lines tracked per site) were also available from December 2002 to November 2016, but only at two sites (Rotoroa and Rotoiti) so mustelid effects were assessed using treatment (trapping yes/no) which was available for all sites and years, rather than stoat tracking rates.

Results

In total, 6690 tracking tunnel observations were used in the analysis. These observations covered an altitudinal range of 463 to 1391 m a.s.l. and average annual beech seedfall levels between 0.71 seeds m⁻² (Rotoiti in 2013) and 7314 seeds m⁻² (Rotoroa in 2000). There were three particularly high-seed (mast) years in 2000, 2006, and 2014 (Fig. 1a), all of which were well above the 2000 seeds m⁻² which triggers likely rodent outbreaks (see Introduction). Rat tracking rates showed marked increases during those high-seed years, except where aerial 1080 was applied prior to monitoring (2014 at Lakehead, Rotoiti and Flora and 2016 at Flora: Fig. 1b). Rat tracking rates were generally highest at Lakehead (stoat trapping but little rat control) and lowest at Rotoroa (non-treatment). Mustelid tracking (Fig. 1c) was higher at Rotoroa than at Rotoiti (stoat trapping).

The GLMM indicates that rat tracking rates were affected by a range of variables (Table 2), with only two predictors having no significant effect (targeted rat-trapping and targeted possum control). Application of other toxins (hand-laid 1080 and pindone) presented a positive response in rat tracking rates (Table 2, Fig. 2). It is unlikely that the use of pindone

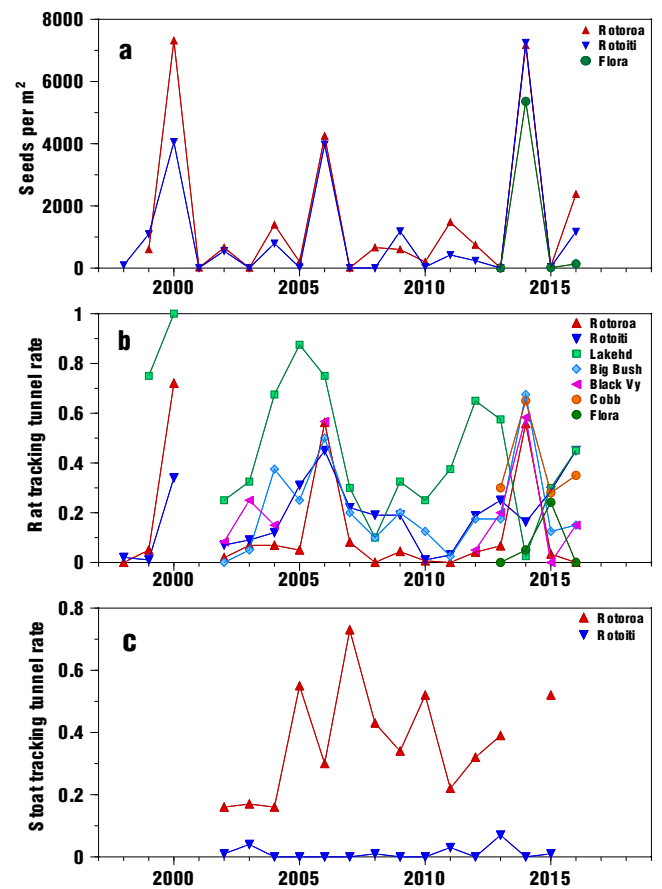


Figure 1. Seedfall and mammal tracking rates during this study. (a) Mean annual beech seedfall m⁻² (*Nothofagus solandri*, *N. fusca*, and *N. menziesii* combined) from Rotoroa, Rotoiti, and Flora. (b) Mean November rat tracking rate (proportion of tunnels) from Rotoroa and Rotoiti. Gaps denote periods when no data were collected. Rotoroa is the non-treatment site; for other site treatments see Table 1.

Table 2. Summary of binomial GLMM predicting November rat tracking rates from rat control (non-treatment, aerial 1080, brodifacoum, diphacinone, other toxins (pindone and hand-laid 1080), and rat trapping), previous year's rat tracking rate, altitude, stoat control (treatment and non-treatment), possum control (treatment and non-treatment), and beech seedfall. Rat tracking rates include data from all sites and years listed in Table 1. Significant p values are indicated in bold.

Random effects	Variance	Std. Dev.		
Tracking tunnel	0.083	0.289		
Tracking tunnel line	0.474	0.689		
Site	0.067	0.260		
Fixed effects	Estimate	Std. Error	z value	P value
(Intercept)	-2.353	0.502	-4.685	< 0.001
Altitude (km)	-1.551	0.463	-3.353	< 0.001
log ₁₀ (Beech seeds m ⁻²)	0.627	0.037	17.070	< 0.001
Previous rat tracking rate	1.523	0.239	6.372	< 0.001
Stoat treatment = yes	1.303	0.379	3.436	< 0.001
Possum treatment = yes	-0.289	0.149	-1.933	0.053
Rat treatment = aerial 1080	-3.110	0.281	-11.049	< 0.001
Rat treatment = brodifacoum	-3.901	1.014	-3.845	< 0.001
Rat treatment = diphacinone	-0.888	0.196	-4.526	< 0.001
Rat treatment = other toxin	0.695	0.190	3.663	< 0.001
Rat treatment = trapping	-0.013	0.149	-0.085	0.932

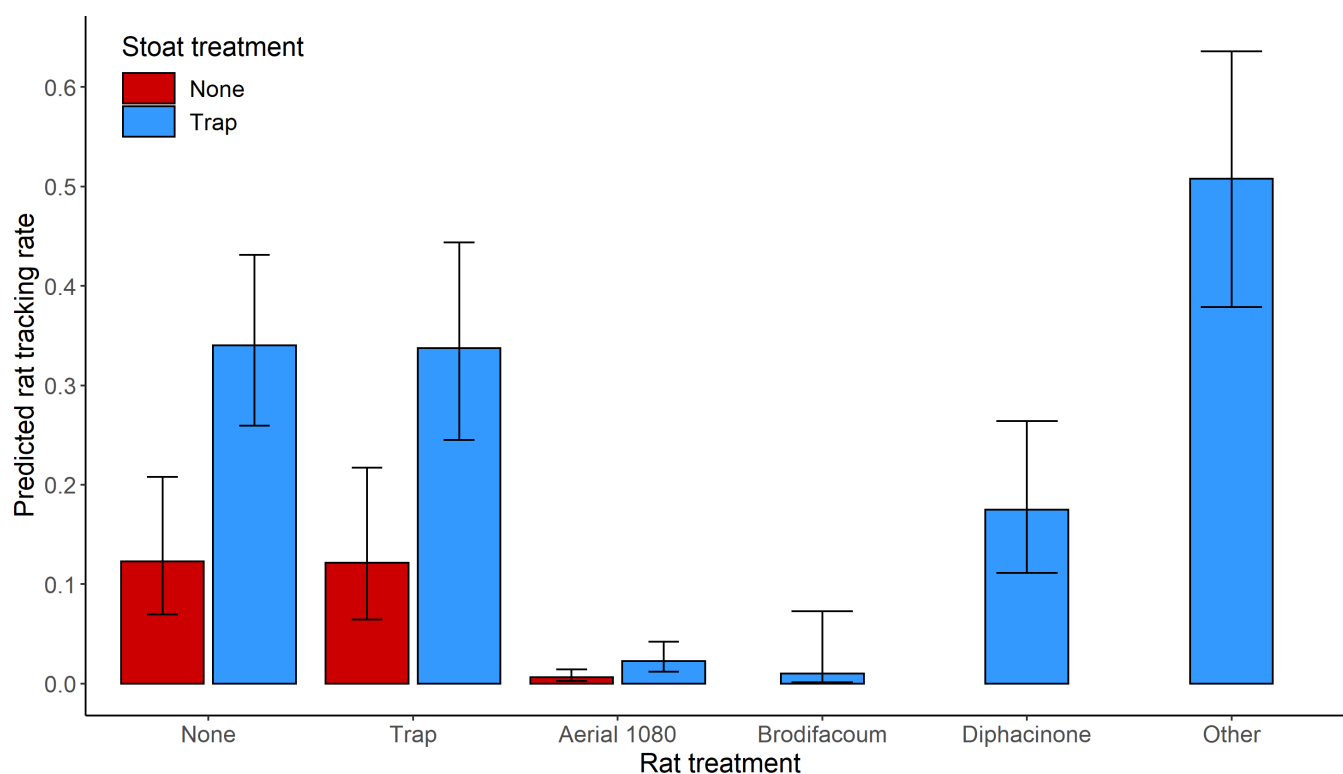


Figure 2. Fitted values for rat tracking rates (proportion of tunnels marked; means with 95% CIs) under different rat treatment regimes, in the presence and absence of stoat trapping. Fitted values assume no interactions between predictors, and are not shown for combinations with no field data; beech seedfall, altitude and previous rat tracking rate were set to their mean values.

and hand-laid 1080 elicited an increase in rat abundance, and more likely that these treatments were ineffective at reducing already-increasing rat populations.

The relative magnitude of significant predictors is shown by the effect sizes (coefficient \times range of the predictor variable), which were largest for brodifacoum, aerial 1080, and seedfall (Table 3). Brodifacoum, aerially-applied 1080, and diphacinone significantly reduced rat tracking rates (Table 2), with both

aerial 1080 and brodifacoum giving proportion tracking rates below the DOC target (Elliott & Kemp 2016) of < 0.05 (Fig. 2). Note that the effect of aerial 1080 was generally measured only a week or two post-treatment and rats would gradually recover thereafter.

When stoats were controlled, ship rat populations increased, reaching particularly high levels at lower altitudes and when *Nothofagus* seedfall levels were high (Fig. 3). The

Table 3. Summary of the relative effect sizes (logit-transformed proportions) for significant predictors of rat tracking rates taken from the GLMM (Table 2). Predictors are listed in order of effect size (coefficient times the observed range from maximum to minimum).

Predictor	Coefficient	Mean	Minimum	Maximum	Effect size
Rat treatment = brodifacoum	-3.901		0	1	-3.901
Rat treatment = aerial 1080	-3.110		0	1	-3.110
\log_{10} (Beech seeds m^{-2})	0.627	2.242	-0.150	3.860	2.514
Altitude (km)	-1.551	0.845	0.460	1.390	1.442
Previous rat tracking rate	1.523	0.184	0	0.875	1.333
Stoat trapping	1.303		0	1	1.303
Rat treatment = diphacinone	-0.888		0	1	-0.888

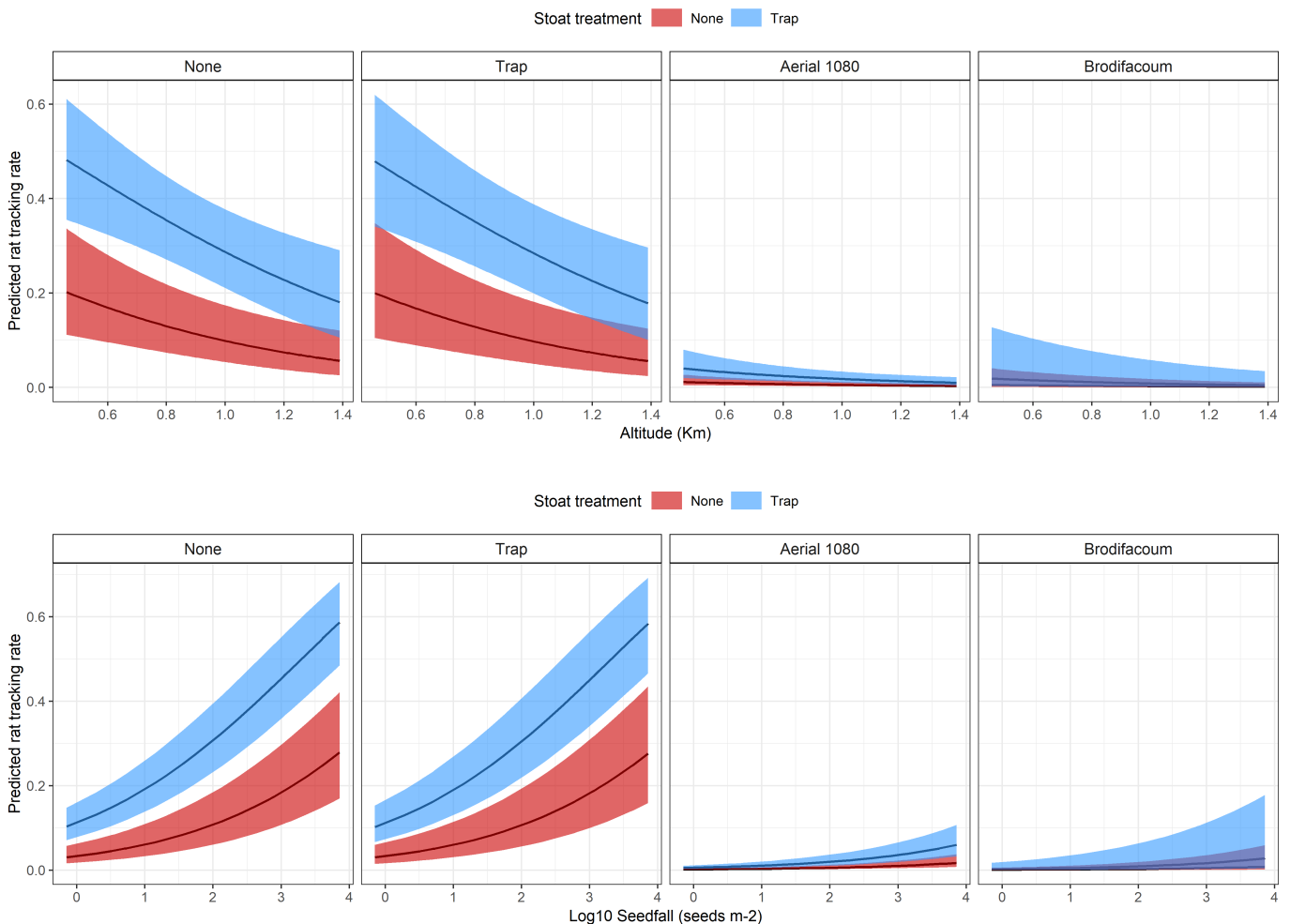


Figure 3. Fitted values for rat tracking rates (proportion of tunnels marked; fitted line with 95% CI) against altitude (top row) and against beech seedfall (bottom row) in the presence or absence of stoat trapping, and with four types of rat control (headers above each panel). Note that these fitted values assume no interactions between predictors, and that some combinations were not run in the field (rat trapping and brodifacoum were not applied in areas without stoat trapping).

fitted values suggest that aerial 1080 and brodifacoum would give lower rat tracking rates in the absence of stoat control, but these fitted values assume no interactions among predictors, and in the field brodifacoum was applied only at sites with stoat control. Thus, further study would be required to determine how these rat treatments interact with stoat trapping.

Discussion

The large data set used here covers an 18 year time span, which has allowed us to identify relationships between ship rat abundance and differing pest control treatments that, until now, have gone undocumented. Although we found some strong effects, there were some limitations of this study that should be noted. Firstly, the experimental design was not ideal, with unbalanced designs and limited replication of some treatments. The experimental limitations restricted some of the effects and interactions that could be examined. For example, we have little power to test possum effects because possums have been controlled, apparently to consistently low levels, at all sites except Rotoroa. Similarly, several other treatments were applied only in areas already receiving stoat trapping. However, what the data lack in design they make up for in quantity, and the design limitations should not invalidate the effects that could be tested. Secondly, we are not testing rat abundance directly, we are using tracking tunnel sign as an index. However, previous work shows that tracking tunnel rates provide a reliable relative index to monitor fluctuations in rat populations (Brown et al. 1996). Thirdly, from tracking tunnel data we cannot identify which *Rattus* species is present, although there is evidence to suggest the rats were probably all *Rattus rattus* (ship rat). Christie et al. (2017) reported on kill-trapping at Rotoroa 1974–1993 and all 118 trapped rats were ship rats. More widely, King (2005) showed that kiore (*R. exulans*) are absent on the upper South Island, and Norway rats (*R. norvegicus*) are almost exclusively commensal, leaving ship rats the dominant forest rat in the northern South Island.

Reductions in rat abundance with increasing altitude and increases after *Nothofagus* seedfall are both previously known, but the altitude effect has only recently been documented (Christie et al. 2017; Walker et al. 2019; Carpenter et al. 2022; Harris et al. 2022). We found rat tracks up to the highest tracking tunnels (at 1391 m in Rotoroa) but tracking rates declined with altitude. This suggests that rat abundance, and hence predation pressure, is lowest at higher altitudes, which affects interpretation of bird abundance changes in response to altitude and pest control (e.g. Elliott et al. 2010). The response to seedfall is also well known (King & Moller 1997; Blackwell et al. 2003; Dilks et al. 2003; Harris et al. 2022) and is the underpinning of the Tiakina Ngā Manu/Battle for our Birds aerial 1080 campaigns carried out throughout the South Island by DOC in the 2014, 2016, and 2019 *Nothofagus* mast years (see www.doc.govt.nz/our-work/tiakina-nga-manu/). Future study of this topic could include testing for an altitude by seedfall interaction, which we were unable to include here due to the unbalanced nature of the dataset. In their longitudinal study at Craigieburn, Harris et al. (2022) found the best fit to rat trap-catch rates was the interaction of temperature and seedfall.

More unexpected than the effect of altitude and seedfall was that stoat control (usually by trapping) was associated with a clear increase in rat tracking rates. Although this mesopredator release was predicted in models by Tompkins & Veltman (2006), analysis of field experiments in the North Island were either equivocal (Blackwell et al. 2003) or found

no evidence for rat increases after stoat control (Ruscoe et al. 2011). The effect in our *Nothofagus* forests was quite clear, as shown by the fact that the lowest rat-tracking rates were nearly always at the non-treatment site, Rotoroa, where stoat tracking rates were high (Fig 1c). The only times that rat tracking rates increased at Rotoroa were for short periods during the three heavy *Nothofagus* seedfall events in 2000, 2006, and 2014, and tracking rates dropped back down within a year after the 2006 and 2014 masting events (there was no rat monitoring in November 2001).

A number of rat treatments were tested. We found no significant effect of snap-trapping on rat tracking rates, despite great effort at Rotoiti in 2000–2005 seeking a trapping intensity which could control rats without the use of toxins. As noted in the Methods, across 825 ha 1042 Victor snap traps were set at various spacings (normally 100 × 100 m grid but sometimes 100 × 50 m) and various checking intervals (typically at 14 day intervals in summer and monthly in winter, but sometimes 3 times per week or even daily). Over 5 years there were 6484 rats caught (Rotoiti Nature Recovery Project Annual Reports 2000/01 to 2004/05, see www.doc.govt.nz), but we found no detectable reduction in local rat tracking rates. This suggests that in large forest blocks, rat trapping is likely to be ineffective at protecting ship-rat vulnerable species. Reducing local rat density to low levels requires both high intensity trapping (high trap density and frequent resetting) and low reinvasion rates. Therefore trapping is most likely to be effective in smaller fragments which have barriers to reinvasion (such as rivers or a fence), and where snap traps can be checked frequently or self-resetting traps (such as the Goodnature A24 trap) are affordable. Reinvasion rates would also be reduced if the treatment was applied over large areas (> 1000 ha), but the cost of intensive trapping makes it impractical at larger scales.

Toxin application was, predictably, far more effective than trapping in reducing rat tracking rates. Brodifacoum was very effective, but use of this toxin was discontinued at RNRP (and throughout managed public conservation land) in 2000 because brodifacoum is persistent and accumulates in the food chain and environment (Eason & Spurr 1995; Eason et al. 1999; Gillies et al. 2003). It is still useful in limited situations, such as a short-term emergency response to a rat outbreak or in island eradications (Empson & Miskelly 1999; Parkes et al. 2011). Aerially-applied 1080 was also very effective (when measured immediately afterwards), and was able to suppress rat outbreaks in response to large *Nothofagus* mast years, even in the presence of stoat trapping. Ground-applied diphacinone significantly depressed rat tracking rates, but was less effective than brodifacoum and 1080. This result is based on the application rates and bait station types used in the few replicates in our dataset, and diphacinone may work better under other conditions. However, aerial 1080 application is currently the preferred option for large-scale rat control, due to its low non-target impacts and high target-species kill rate (Parkes et al. 2017). Our study supports maintaining or increasing the frequency of aerial 1080 use for rat control, especially in sites and years with mustelid trapping operations in place and high rat densities. If 1080 operations have to be repeated after a short interval, learned aversion by rats may be an issue, which may need to be managed by changing bait appearance and taste (Nugent et al. 2019).

Overall, this analysis has confirmed a number of previously known or suspected factors affecting rat tracking rates, and has shown that (in contrast to the situation in mixed North Island forests, Ruscoe et al 2011) rat tracking rates in Nelson

Nothofagus forests increased with stoat control. Since stoat control is relatively easy, and rat control very difficult, land managers (including community groups) must carefully balance the relative threats to native wildlife from stoats and ship rats when deciding whether to trap stoats in *Nothofagus* forest areas. Trapping stoats is likely to protect some large native stoat-sensitive species (including kākā *Nestor meridionalis*, kiwi *Apteryx* spp., and whio *Hymenolaimus malacorhynchos*) but at a possible cost to greater predation on rat-sensitive smaller species (including mohua *Mohoua ochrocephala*, kakariki *Cyanoramphus* spp, rifleman *Acanthisitta chloris*, and robins and tomtits *Petroica* spp.) (Innes et al. 2010).

Our final comment is to call attention to the great value of long term datasets, here collected in a consistent way across large areas of old-growth *Nothofagus* forest in the Nelson-Golden Bay region. Other examples include very long-term seedfall data used in Kelly et al. (2000), Schaubert et al. (2002), Kelly et al. (2013), Christie et al. (2017), and Harris et al. (2022), and bird count data used in Elliott et al. (2010) and Rossignaud et al. (2022). The value of these data for revealing long term trends cannot be overstated. The Rotoroa site at Mt Misery deserves special recognition, because Mt Misery is almost the only large patch of well-monitored native forest in New Zealand where no pest control of any kind has been undertaken. Overseas, such long-term ecological monitoring sites are recognised with dedicated funding (e.g. the NSF's Long Term Ecological Research sites in the USA). Such sites deserve higher recognition and more secure funding within New Zealand.

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Author contributions

DK and KW conceived the study; KW, TG, AM, JVV and KD collected the data; KW, DK, JVV and LR ran the analyses; KW and DK wrote the draft, and all authors helped revise the manuscript.

Data and code availability

The tracking tunnel data are archived in the Department of Conservation tracking tunnel database (contact person: Josh Kemp). The TT data are also available from the corresponding author, as is the R code.

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